

**ANTHOPHORA PILIPES VILLOSULA SM. (HYMENOPTERA:  
ANTHOPHORIDAE), A MANAGEABLE JAPANESE BEE THAT  
VISITS BLUEBERRIES AND APPLES DURING COOL, RAINY,  
SPRING WEATHER**

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*Abstract.*—The vernal, univoltine solitary Japanese bee, *Anthophora pilipes villosula*, promises to be a worthy addition to our pollinator fauna. It was easily maintained in inexpensive, portable adobe blocks. It is gentle, forages during inclement weather, also from before dawn until after dusk in fine weather. It is polylectic, does not steal nectar, flies rapidly, forages to 500 m, visits numerous flowers including blueberry and apple, and sonicates. Its active period coincides well with spring fruit blossom in the temperate zone. Females may make several nests, learning new nest locations. Dormant nests in adobe blocks were kept outdoors through five years in Maryland with minimal insulation, and the population approximately tripled each year. Details are provided regarding its behavior in Japan and Maryland, including phenology in relation to crops, wild plants and other bees, hosts, foraging behavior, effects of weather, management, substrate and nesting behavior, territorial behavior of males and mating.

*Key Words:* Pollination, bee, apple, blueberry, bionomics, management, Japan, U.S.A.

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This report concerns the biology of a dynamic pollinator that efficiently utilizes the abundant floral resources of spring, discusses its limiting environmental factors, and its potential management for the pollination of crops that bloom in the spring. Honey bees are versatile, manageable pollinators for most crops, and they also provide us with valued honey and wax, but they are not the best pollinating species for all crops, under all conditions. For example, they do not perform as well as bumble bees and some solitary bees in cool or rainy weather. They fly relatively slowly, and they have morphological limitations or behaviors that make them less efficient than some other bee species as pollinators of certain crops, including alfalfa, red clover, 'Delicious' apples, blueberries, huckleberries,

cranberries, tomatoes, potatoes, eggplants, peppers, cotton, okra, and many crops that are grown in greenhouses (Boyle and Philogène 1983, Parker et al. 1987).

Blueberries are particularly poorly pollinated by honey bees. The short spring flowering season is often rainy or cool, and honey bees do not sonicate, which pollinates blueberry flowers efficiently. Because populations of the well-adapted and effective native blueberry pollinators are often low, due to habitat destruction and pesticides, growers may saturate their blueberry fields with honey bees in order to achieve adequate pollination. Nevertheless, rainy weather may prevent these honey bees from foraging.

Doubts about the effectiveness of honey bees arose early during the development of

blueberries as a cultivated crop. Shaw et al. (1939) made detailed field observations and performed controlled pollination trials in cages during three years. These revealed that bumble bees were the most abundant pollinators, and that individual bumble bees were three times more efficient as pollinators than individual honey bees. Subsequent studies have confirmed the superior efficacy of bumble bees. Now their populations have declined in many areas (Bigras-Huot et al. 1973, Finnamore and Neary 1978, Plowright and Laverty 1987 and references therein).

The flowers of blueberries (highbush, lowbush, rabbiteye, and others in the section *Cyanococcus*) have pendant, inverted, globose to urceolate corollas. A flower's nectaries and anthers are accessible only through a small ventral hole. This structure requires pollinators to hang upside-down while probing into the hole. The poricidally-dehiscent anthers do not readily release their pollen. Bees use three methods to obtain nectar, pollen, or both, from these flowers: 1. Nectar-robbers cut slits at the top of the corolla, through which they sip from the nectaries, but these do not accomplish any pollination, because anthers and stigmas are not contacted. Carpenter bees (*Xylocopa* spp.) usually make these slits, but honey bees, bumble bees and *Andrena* bees soon learn to use them. The widespread use of robber slits by honey bees may have been responsible for recent poor blueberry yields in Florida (Morse 1991). 2. Pollen-grabbers reach into the ventral pores with their mandibles and front legs, to bite the anthers, loosen the pollen, and rake it out, while imbibing the nectar. This method is used by many species of andrenids, halictids, megachilids, and honey bees. Some pollination is accomplished, but these bees usually work slowly. 3. The most efficient technique to loosen, collect, and transfer the pollen is buzz-pollination or sonication. A foraging bee, after alighting, positions the ventral side of her thorax over the pore and shivers her

thoracic flight muscles without fanning her wings, producing a distinct buzz. Certain species that are capable of sonication belong to several genera, including *Colletes*, *Andrena*, *Melitta*, *Augochloropsis*, *Xylocopa*, *Bombus*, *Amegilla*, *Tetrapedia*, *Habropoda*, *Anthophora*, and some other anthophorids.

Bumble bees have been artificially reared for many years, but no method provides a large number of foragers early in spring when bees are most needed for blueberry pollination. New bumble bee mass-rearing techniques may ameliorate this shortage eventually (Plowright and Laverty 1987). *Colletes validus* Cresson is a native solitary bee that specializes on blueberries and sonicates their flowers. Pheromones may be used to assist relocation of their nest sites, but more research is needed (Batra 1980). Torchio (1990) found that the native megachilid, *Osmia ribifloris biedermannii* Michener is a good blueberry pollinator, and it is potentially manageable. Cane and Payne (1988, 1990) found that the "southeastern blueberry bee," a native anthophorid, *Habropoda laboriosa* (F.), is an excellent sonicating pollinator of rabbiteye blueberries in the southern states. Techniques to manage its populations are needed. Because the timing of the adult activity of this species coincides with blueberry bloom and they have little need for other floral resources, these bees are superior to bumble bees for blueberry pollination. Their relatively short foraging range is beneficial because they stay in the blueberry fields. Further research concerning the conservation, enhancement, and movement of large populations of these three solitary blueberry pollinating species would be beneficial.

*Anthophora pilipes villosula* for brevity is referred to as *A. pilipes* in this report. This follows the revision by Day (1979), although in Europe it is often named *A. acervorum* (L.), a synonym. In Sasayama, Hyogo Prefecture, Japan, it is polylectic and visits a wide variety of hosts from April to June, including species of *Astragalus*, *Wis-*

*taria*, *Corydalis*, *Eleagnus*, *Viola*, *Rhododendron*, *Glechoma*, *Ajuga*, *Lamium*, *Brassica*, *Rosa*, *Potentilla*, *Chaenomeles*, *Rubus*, *Taraxicum*, *Weigela*, *Abelia*, *Ranunculus*, *Xanthoxylum* and *Mazus* (Miyamoto 1958, 1960, 1962). In the temperate forest at Kibune, near Kyoto, Inoue et al. (1990) found it on *Corydalis*, and Kakutani et al. (1990) found it visiting *Rhododendron*, *Lonicera* and *Viburnum* in Kyoto. Murakimi and Itino (1990) found that *A. pilipes* preferentially visited *Astragalus* early in the morning and late in the afternoon, when the flowers yielded the most abundant nectar. In Europe, *Anthophora pilipes* forages on 93 species of plants, from the end of April until early June; *Lamium* spp. are preferred hosts (Malyshev 1928, Thalmann and Dorn 1990, Westrich 1990).

The nesting behavior of *A. pilipes* in Japan was first investigated by Torikata (1931), who found that the oval, 10–15 cm long brood cells formed an oblique series of up to four cells. Each cell was about half full of semiliquid provision. Parasites were *Meloe carinus* Marseul, *Monodontomerus japonicus* Ashmead, and *Saproglyphus neglectus* Berlese. In Hyogo Prefecture, Miyamoto (1958) found *A. pilipes* nesting gregariously in the adobe wall of a cottage and in a dry cliff. They were active from April 17 to May 17. Some females made more than one nest, and they preferred to reoccupy and refurbish an abandoned old nest rather than to construct a new nest. Thus some burrows contained cells that were made by more than one individual. Males slept in burrows and patrolled the nest aggregations. *Astragalus sinicus* L. was the preferred host at this location. Togashi (1990) noted *A. pilipes* nests in the adobe wall of an old thatched college in Ishikawa Prefecture.

*Anthophora pilipes* also live in adobe walls in Europe. Fabre (1920) observed their gregarious nests in adobe, and noted the nauseating odor of the bees' provisions. Malyshev (1928) also found *A. pilipes* nests in

adobe walls, and he made detailed observations of nests constructed in adobe blocks. Van Lith (1947) found them nesting as a perennial aggregation in dry, sandy clay soil beneath a verandah. The nearly vertical brood cells were in series and they were lined with a thick, whitish-gray waxy substance. Cells were half-full of provisions bearing eggs or young larvae in early May. Pupation began by July, and young diapausing adults appeared in September. The inquiline, *Mellecta punctata* (F.) was present. The pungent, rancid odor noted by Fabre (1920) probably is that of butyric acid, which is liberated from triglycerides in the provision and the cell lining, probably secreted by the abdominal Dufour's gland, as in other *Anthophora* bees (Norden et al. 1980).

Recently, Thalmann (1991) and Thalmann and Dorn (1990) investigated the biology of *A. pilipes* and its management as a crop pollinator in Germany. In 1988 and 1989, they tested various soil textures and moisture levels, to determine how they may affect nesting success, and they developed portable blocks of soil for use by growers. They found that provisioned cells became moldy when soil moisture was high. They were also favorably impressed by the potential usefulness of this bee, which has such assets as a long glossa, long daily foraging period (up to 18 hours), ability to work during cool (8–9°C) and sunny (20,000 lux), or during warm (20°C) and cloudy days, as well as early and late in the day, from 4:00 at 600 lux to 21:00 at 300 lux. They noted that it was active in spring before bumble bees produced workers, its polylecty, the long active lives of individual females, and the large numbers of flowers visited for provisions (for example, 2500 *Brassica* flowers were visited to make a 522-mg pollen mass). In Germany, adults flew from the end of April until early June, eggs hatched 1–2 days after laying, larvae matured (at 400 mg) after 4 weeks, pupation occurred 70–80 days after oviposition, and diapausing adults appeared in September. Parasites were *Mon-*



*odontomerus obscurus* Westwood and *Mellecta punctata*.

#### MATERIALS AND METHODS

The equipment that was used was simple and inexpensive. It included a 35 mm SLR camera with macro lens, high speed film, stopwatch, watch, photovoltaic light meter, thermometers, insect net, quick-drying enamel, cages, microscope, etc. The adobe substrate for nesting was made of the local red marine clay. This fine-grained, acid natural clay was put into wooden, metal, or styrofoam boxes of various sizes but small enough to be portable by one person when full of clay. The clods were chopped, mixed with water and pressed; the surface was smoothed and allowed to dry thoroughly for several weeks, forming a very hard, brick-like adobe 15–20 cm deep. Before dry, 10–15 smooth holes, ca. 1 cm diam. × 5 cm deep, were punched into the moist adobe; these attracted nest-seeking bees. The adobe blocks were placed under rain shelters, with a southerly exposure. They could be used singly, or stacked to form a wall, with the adobe face exposed. The white polystyrene boxes (= insulated shipping containers) were most satisfactory, being waterproof, lightweight, and providing them some insulation. The adobe blocks were durable and maintenance-free, remaining uncracked after 4 years, even when riddled with bees' nest tunnels. Gray squirrels destroyed some adobe and bees' nests in 1992, so protection during dormancy is recommended. Nests were color-coded and numbered sequentially each year as they were constructed by the bees.

#### BEHAVIOR IN JAPAN

Research on the biology and management of *Anthophora pilipes villosula* Smith (det. Y. Maeta) began incidentally, while I was in Japan working with other projects. I had rented a century-old farm house in Higashi Mochida Cho, just outside Matsue, Shimane Prefecture. This location is in humid,

subtropical southwestern Honshu, Japan (36°N). Early during my first morning in this house (May 15, 1988), I heard loud hums originating below the tatami floor. On investigation, I found an aggregation of eight nests of this bee in the adobe wall that supported the lower part of the western wall of the house. This adobe was made of dried ochre clay mixed with chopped rice straw. The bees' nests were behind some loose roof tiles that were leaning against the wall. Very impressive were the continuous swift flights of this species, its willingness to fly during light rain, as well as in cloudy or cool weather, and its long daily period of flight, from before sunrise to until after sunset. I immediately thought that this species might be a valuable addition to our North American pollinator fauna. Its habit of nesting in adobe indicated that it could be managed for crop pollination relatively easily. *Anthophora parietina* F. has been managed in Europe for legume pollination; it also nests in adobe (Wojtowski 1964).

Because it was already late in the bees' flight season, which ended on May 29, it was possible to make only a few observations of foraging behavior in Japan. Females foraged for nectar and pollen on red azaleas (*Rhododendron* sp.) in the garden. They also collected pollen from the pendulous white flowers of *Styrax japonica* Sieb. & Zucc., a small tree in this area. The bees hung upside-down and sonicated the *Styrax* flowers to release their pollen. Thus, I was reminded of similar pollinator behavior on blueberries. There were no blueberries in the area, so it was not possible to study the bee pollinating this crop. Sugden (1986) observed bumble bee queens pollinating a North American species of *Styrax*. Although he did not mention it, sonication probably occurred.

A total of nine hours from May 15 to 29, 1988, were spent observing *A. pilipes* behavior in Japan. Matsue is climatically similar to coastal Georgia (Nuttonson 1949), or approximately comparable to USDA Plant

Hardiness Zone 8. Vegetation in the area includes bamboos, camellias, palms, *Cryptomeria*, kumquats, loquats, kaki, *Styrax*, and azaleas. The nest site, which was near sea level in the village, was surrounded by rice fields set amid steep, densely forested mountains.

Foraging females began flights as early as 5:03, 15 minutes before sunrise, and they remained continuously active until 19:30, after sunset. Morning activity began at 10°C, when the nest site received only 150 lux, although the brightest part of the visible sky to the east registered 2000 lux. The nest entrances, which were covered by the roof tiles, received only 10 lux at dawn. In the evenings of clear days, the bees ceased their activity when the brightest part of the sky to the west, visible at the nest site, registered 100 lux. The general appearance of the landscape when the bees began and ended their flights was grayish, although some bright colors were still somewhat visible to the human eye.

The females collected pollen from at least three hosts, judging from the colors of their pollen loads. They continued to forage during light rain. When the roof tiles that covered their nest entrances were removed, six returning foragers became confused, and refused to enter their newly-visible nests. When these tiles were replaced, they promptly entered nests. Evidently the tiles were important landmarks, even though they concealed and darkened the nest entrances. The nests and their surroundings had a distinct cheesy or butyric odor, and a few *Monodontomerus* sp. were present. Captured females emitted a penetrating citronella-like odor from their mandibular glands. According to Y. Maeta, (pers. comm.), this species is active from April 8 to June 11 in Shimane and Fukuoka Prefectures. Bees that nest in the adobe walls of village houses are tolerated by the occupants, because these bees are not aggressive. However, large numbers of bee tunnels may cause the collapse of such walls.

#### ESTABLISHMENT

Because their potential as manageable crop pollinators is good, a permit for importation into the United States was obtained from APHIS, and in December 1988, Dr. Maeta shipped 109 diapausing adults in cells to the USDA Beneficial Insects Research Laboratory at Newark, Delaware. These had been collected at Sugata-Cho, Matsue. Some adults had emerged from their cells during shipment. Those that lived were placed in gelatin capsules to resume their diapause. Unopened cells were cracked open, to check for dead bees or parasites, which were destroyed in quarantine. After microscopic inspection, all 56 diapausing adults in capsules or cells were stored at 3°C, until April 1989.

Two Saran screen cages (4 × 4 × 2 m) were set up over a dense growth of wild, understory lowbush and highbush blueberries, deerberries, and huckleberries in the oak-pine forest at Beltsville. Each cage contained a small rain shelter over an adobe block. They were set up under the rain shelters at ground level and facing south. The cages contained various cut plants, including apple, crabapple, azalea, mustard, and other flowers. Cultivated blueberry varieties growing in pots were also placed in the cages. Water in shallow trays was provided for nesting females, but they were never seen to collect water.

During the evening of April 18, 1989, the cells and capsules containing bees were placed in the cages. They were put next to the adobe blocks, so that emerging bees would perform their first orientation flights at these blocks, thus memorizing their locations. Bees began to emerge within 15 minutes, and most of them immediately flew up to the roofs of the cages. By the next morning (April 19), many of the bees had adjusted to the confinement of the cages, and both sexes were foraging on cut azalea, crabapple and narcissus. Males had begun to closely pursue females in flight, pouncing

on them when they alighted on flowers. Males were already attracted to the holes in the clay blocks, which they patrolled and inspected while hovering, although no females had yet occupied the holes or the adobe blocks. By the end of this first day, both sexes expertly and rapidly darted through small gaps in the vegetation and they avoided hitting the cage mesh or other objects. This facile adaptation suggested that this species may be suitable for use in greenhouses or other confinement, where honey bees do not thrive.

By April 21, after a rainy day, males and females had begun overnight occupancy of the holes in the adobe blocks. On emerging in the morning, they performed normal orientation flights. Some bees also slept in the open, while grasping twigs or the cage mesh by their mandibles. The first female was seen to excavate a nest burrow on April 25. It was started in a hole in the adobe. By April 27, several females were nesting in the adobe blocks in the cages.

Details regarding phenology, pollination, mating and nesting behavior during five years are discussed below. In 1989, emergence was somewhat delayed due to prolonged refrigeration, but the data for 1990, 1991, 1992 and 1993 reflect the bees' normal behavior under prevailing environmental conditions at Beltsville during those years. A total of 339 hours were spent observing *A. pilipes* in Maryland between April 18, 1989, and June 9, 1992; a few additional observations were made in 1993.

#### PHENOLOGY OF THE BEES, THEIR HOSTS, AND THEIR ASSOCIATES IN MARYLAND

In the Beltsville area, red maple (*Acer rubrum* L.) is a dominant species that indicates the onset of spring. It is the first major food source for bees to appear each year (Batra 1985). In 1989, 1990, 1991, and 1992, male flowers began to bloom on February 5, February 9, February 12, and March 5, respectively. The earliest of the solitary bees, *Andrena fenningeri* Viereck, made its first

appearance (males) on March 14, February 9, February 12 and February 28; *Colletes inaequalis* Say males first appeared on March 14, March 13, March 1, and March 2; males of the introduced Japanese pollinator *Osmia cornifrons* Radoszkowski began emerging on April 18, March 10, March 27, and March 31, respectively (Fig. 1). Apples began to bloom on April 20, March 28, April 9, and April 22; highbush blueberries similarly began blooming April 19, March 22, April 8, and April 14 (Fig. 1). The artificially delayed emergence of *A. pilipes* began on April 18 in 1989, but it began on March 15, 1990, March 26, 1991, and March 27, 1992, after overwintering in a sheltered area at ambient winter temperatures. The first bumble bee queens were also seen on the latter two dates. The more numerous, pollinating bumble bee workers appeared a month later, but by then the blueberries and apples had almost finished blooming. The well publicized blooming of the Japanese cherry trees during five years at the Tidal Basin in Washington, D.C., proved to be a reliable indicator for the time of emergence of *A. pilipes* in nearby Maryland, which is slightly cooler than Washington. Thus, in 1990 when the cherry trees bloomed earlier than usual, *A. pilipes* also emerged early (Fig. 1). The flight period and maximum abundance of *A. pilipes* coincided well with the flowering of apples, blueberries, pears, plums, and cherries. It ended soon after the end of blueberry bloom. By then, most females had died, and the forest canopy had fully leafed out (Figs. 1, 2).

Males of the local native species, *Anthophora abrupta* Say, were just beginning their annual activity after the canopy had leafed out (mean emergence date for males June 10; females June 15 (Norden, 1984)). The active period of *A. pilipes* does not overlap significantly with this native species of *Anthophora* and local *A. bomboides* Kirby. There should be almost no competition for food, which is abundant in spring.

Parasites of native bees may transfer to



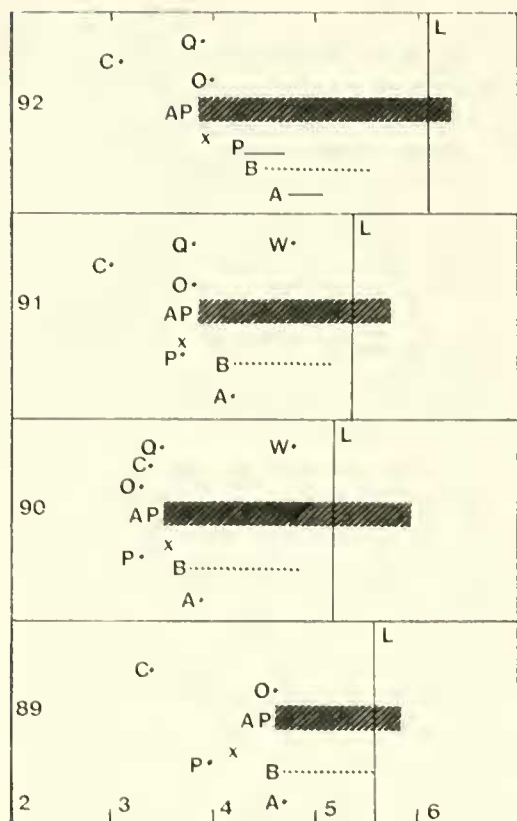


Fig. 1. Phenology of *A. pilipes*, the vernal flowering of plants, the status of the forest canopy, and the emergence of other pollinators from February (2) through June (6) of 1989, 1990, 1991 and 1992 at Beltsville, MD. Vertical bars (L), times when canopy was fully leafed out; AP bar, period of activity of *A. pilipes*. First emergences of other bees are: C, *Colletes inaequalis*; O, *Osmia cornifrons*; Q, *Bombus queens*; W, *Bombus* workers. The beginning of bloom or flowering periods of pear (P), highbush and lowbush blueberries (B), and apple (A) are shown; X indicates the full bloom of ornamental Japanese cherries at the Washington, D.C., tidal basin.

*A. pilipes*. On May 27, 1991 and June 8, 1992, several *Monodontomerus mandibularis* Gahan (Torymidae) were attracted to *A. pilipes* nests and reproduced there. This species, which usually attacks native anthophorid bees such as *A. abrupta* (Rau 1947), may become a pest of managed *A. pilipes*. It could be avoided by removing the nests to storage after mid-May, when few *A. pilipes* females



Fig. 2. The number of entrances of inhabited nests in April (4) and May (5) 1990, 1991, and 1992. Many entrances are shared by two nesting females after late April so that the number of entrances does not reflect the number of nests, thus the curve levels off somewhat. Note the rapid increase in nests in early April, 1991 and 1992 (to arrows), when the weather was warm and sunny. The period of peak nesting activity coincided well with apple and blueberry bloom in all years.

are still nesting. In 1992, one female that had died at the nest site contained an unidentified conopid larva.

#### INFLUENCE OF TEMPERATURE, LIGHT AND RAINFALL

**Temperature:** Diapausing bees in Maryland overwintered successfully in their cells in the adobe blocks for 3 years. These were kept outdoors at ambient temperatures throughout the year, while temperatures ranged from above  $+40^{\circ}$  to below  $-20^{\circ}\text{C}$ . The dormant nests were protected from rain, and they were also insulated from both the summer sun and the cold north winter winds by a layer of polystyrene covered by wooden boards, which were removed in March, before the bees were due to emerge. In Shimanu, the climate is less extreme than that in Maryland.

Adults began emerging in spring while nocturnal frosts still regularly occurred, and there were some snowy days during their flight season. For example, in 1991, the males began to emerge on March 20, but it snowed during the following night. From March 26–28, both sexes were active, the females began nesting, and apples began to bloom, but then it snowed several cm during April 6–7. Usually bees avoided the frosts by retreating to their burrows and other holes. When chilled, resting bees of both sexes vigorously pumped their abdomens (2/s) and visibly shivered their flight muscles, apparently thus endothermically warming themselves in preparation for flight. A related species, *A. plumipes* (Pallas) has by far the highest metabolic warm-up rate among 52 bee species in six families tested; this permits them to begin flights in cool weather (Stone and Willmer 1989).

The threshold for initial morning flight activity at insulated nests in Maryland after a frosty night was 9.0°C, with clear sky at 3000–3500 lux visible from the nests. Predation by birds may occur at such low temperatures, when these normally alert, active bees are sluggish. In Japan, females began foraging before dawn on clear days at 10°C and 2000 lux. Once started, flight activity continued at air temperatures of 7.0–7.5°C when bumble bees, honey bees and other bees were inactive. On April 2, 1992, both sexes swarmed back to their nests through wind and snow flurries at 3.5°C when clouds suddenly appeared. They had been flying through ambient air at 7°C to forage on sunlit forbs in a 15–17°C microclimate within 6–15 cm of the soil surface. As the females aged, they became relatively less active in cool weather, and subject to predation by birds. For example, on May 7, 1992 at 11°C, only three foragers were seen returning with pollen during five minutes at mid-day. During recent warm days, or during cool days when they were young, there was far more foraging activity.

*Light:* On warm, clear days, the bees be-

gan foraging about 30 minutes before sunrise, and continued foraging until well after dusk. The evening threshold for bees to leave nests on foraging trips was 70 lux, even though the returning foragers had difficulty locating their nests. At low light levels (600 lux), the bees flew hesitantly and slowly, emitting a soft low-pitched buzz, and with prolonged hovering orientation. Some returning bees alighted on the clay surface and then crawled into their nests; normally in bright light, bees enter nests directly and rapidly.

*Rainfall:* This species foraged for nectar and some pollen in the rain at 15°C at 1600 lux, when other bees did not, including bumble bees, *Osmia cornifrons*, and honey bees. In light, steady rain or drizzle, at 10°C, *A. pilipes* regularly foraged for nectar on soaking-wet azalea flowers. During a thunderstorm, which interrupted their busy afternoon, foragers continued to leave nests at 190 lux beneath the lowering, dark clouds. They flew straight into the downpour before they apparently realized their mistake and promptly returned to their sheltered dry nests. *Anthophora abrupta* also forages during light rain (Norden 1984). *Anthophora crinipes* Smith was able to locate its nests inside a dark barn (Grozdanic and Mucalica 1969), and I noted that *A. pilipes* females that had accidentally entered my house flew about normally in dim light. The foraging performance of *A. pilipes* in rain was superior to that of local bumble bees and their activity level was similar to that of Arctic bumble bees, which regularly forage in light rain at 100–300 lux (Lundberg 1980). The Australian anthophorid bee, *Amegilla dawsoni* (Rayment) also forages from before sunrise until after sunset, at temperatures as low as 7°C, and in light rain (Houston 1991).

#### POLLINATING BEHAVIOR AND HOSTS

In Maryland, *A. pilipes* visited the following hosts (N: females or males taking nectar; P: females collecting pollen): *Rhododendron* spp. cv, N & P; pinxter, *Rhododendron nu-*



*diflorum* (L.) Torr., N & P; apple and crabapple cv, N & P, 18 flowers per min; redbud, *Cercis canadensis* L., N; *Brassica rapa* L., N & P; *Kerria japonica* (L.) DC., N & P; *Robinia pseudo-acacia* L., N & P (with sonication); *Lonicera tatarica* L., N & P; *Lonicera fragrantissima*, N; *Lonicera japonica*, Thunb. N; *Paeonia* cv, P; *Chaenomeles japonica*, Lindl. N; *Pulmonaria* cv, N; *Narcissus* cv, N; *Viola papilionacea* Pursh. N; *Taraxicum officinale* Weber. N; *Dicentra spectabilis*, L. N; *Ajuga reptans*, L. N; *Pieris japonica*, N & P (sonication); *Lamium purpureum* L., N & P; *Viburnum carlesii* cv, N; *Vinca minor* L., N; wild *Vaccinium corymbosum* L., N, 13 flowers/min and N & P (with sonication) 18–25 flowers/min; wild *Vaccinium vacillans* Torr., N & P 18–25 flowers/min; and cultivated hybrid blueberries. All hosts were legitimately visited, and there was no nectar robbing.

Wild and cultivated *Rhododendron* were preferred pollen and nectar sources for these polylectic bees, and males patrolled bushes where females were foraging that were 300 m from the nests. One individually marked female regularly flew one km roundtrip to forage on a patch of early-blooming azaleas, bypassing later-blooming bushes nearer to the nests, which were being visited by other females. Possibly this bee was exhibiting site fidelity, having been initially attracted by the early bloom. Because of this preference, *A. pilipes villosula* may popularly be called "azalea bees." In North America, *Rhododendron* spp. are pollinated mainly by bumble bee queens (Lovell and Lovell 1932). The flight range of *Anthophora abrupta* is at least two miles (Rau 1931).

Pollen loads taken from 26 bees entering nests at two locations were microscopically analyzed. At one suburban location, apples, crabapples, azaleas, *Lonicera tatarica* and various ornamentals were in full bloom. At the second location, highbush and lowbush wild blueberries in full bloom formed the understory of a forest; crabapples and several flowering weeds, including *Lamium* and

*Brassica*, grew in nearby fields. At the suburban location, five of nine sampled bees had collected apple or crabapple pollen; their loads contained 20%, 50%, 80%, 90% and 100% of this pollen. Many of these apple pollen grains and other pollens from scopae began to germinate when held for a few hours in glass vials. Suburban bees collected pollen from at least seven hosts; individual loads contained pollen from 1–4 hosts. At the forest location, two of 17 bees included blueberry pollen in their mixed pollen loads. Bees visited the fields to collect crabapple pollen and the distinctive orange pollen of *Lamium purpureum*, as well as pollen from four additional hosts. Foragers collecting nectar and pollen from apple flowers always stood on the anthers, which is the most effective position for pollination.

During a day's foraging, and during the course of several days' foraging needed to provision several cells and complete a nest, some individually marked bees returned with series of pollen loads of the same color and texture, others alternated loads of different colors, or brought back pollens of two or more colors in the same load. Foragers changed pollen sources (colors) over time, as new hosts came into bloom. Several sequential bee trips may return with pollen, or foragers may alternately return with pollen or without it (presumably with nectar). As each cell neared completion, the foragers returned without pollen, bearing liquid to be regurgitated and used to complete and seal cells. They often approached their nests with their probosces extended.

Several new cultivated blueberry varieties that were being developed at Beltsville were tested during three weeks in 1989 in cage studies. Both males and females readily visited the flowers for nectar, and the females sonicated all varieties to collect the pollen. No nectar-robbing was seen, and no holes were cut in any of the hundreds of caged blueberry flowers. Flowers varied greatly among varieties in shape and accessibility to bees. Surprisingly, T-339, the va-

riety with the narrowest ventral hole, was the most attractive to *A. pilipes* foragers. Its holes, 1.5–2.5 mm in diameter, were largely blocked by its stigmas. Nevertheless, foragers pushed the stigmas aside and inserted their long glossas into the nectaries, while they buzzed loudly to release the pollen (the buzz was audible from two m). They visited 12–15 T-339 flowers/min. Variety G-139 Converse, which had more accessible nectar, with a hole of 4–5 mm, was less attractive. The bees worked 12 of the globular flowers of this variety per minute. Other varieties that foragers visited for nectar and pollen were G-600; T-117; G-494; T-460 (10/min); and T-256 (a late bloomer). These visitation rates include the time spent flying between widely spaced flowers and crawling between clustered flowers. Foragers packed the pollen into their scopae while probing, flying, or hanging from flowers. It is interesting that this bee, which probably did not coevolve with *Vaccinium*, proved to be such an effective pollinator, and that its behavior on *Styrax* was a good predictor of success. Maeta et al. (1990) subsequently confirmed that *A. pilipes* is a superior pollinator for cultivated blueberries.

#### BEHAVIORS OF MALES

*Emergence:* The first male *A. pilipes* emerged one to ten days before the first females appeared; such proterandry is characteristic of solitary bees. The spread between the dates of emergence of males and females each year appeared to depend on transient weather conditions. The first sign that the bees were about to emerge each spring was the appearance of small (ca. 0.5–2.0 mm) holes in the hard, shiny earth that sealed the nest entrances throughout dormancy. These pinholes remained unchanged for several days to three weeks before the nest occupants began to emerge. The males were responsible for breaking open the nest seals. Their small mandibles appear to be weaker than those of female bees but they softened the soil with liquid

from the glossa. An emerging male may take up to an hour to chew through the nest seal.

Once exposed, the young, dust-covered males at first rested at their nest entrances for 2–3 minutes, then they suddenly began to jerk their heads from side-to-side and wiped their faces, antennae, and protruded glossae repeatedly, using their front legs. These males then abruptly ceased their grooming and left their natal nests, to perform spiraling orientation flights that lasted 20–30 seconds. Such flights formed ever wider, higher arcs, while the males faced toward their nest entrances, before disappearing. One male crawled out and faced toward his natal nest before beginning his orientation flight. Males returned to the nests after 30–40 min, where they began to patrol briefly (10–50 s visits), and began to chase each other (Fig. 3), even though no females had yet emerged.

*Territories:* From before dawn to after dusk, male *A. pilipes* jointly patrolled territories that included floral hosts, such as bushes up to 300 m away from nests, and the area around the nests. Individual (marked) males alternated between these sites at different times of day, or on different days, throughout their lives. Males occasionally alighted in the sun to bask or to rest for a few seconds, and they stopped at flowers briefly to forage. At these times, objects delimiting the territory may be marked with the male's scent. No scent could be detected on the hairs of the mid and hind legs of male *A. pilipes*, but their mandibular glands produced a distinct unidentified geraniol- to citronellal-like odor that resembles that from female *A. pilipes* mandibular glands. Vinson and Frankie (1990) found that *Xylocopa* bees rub volatile mesosomal gland secretion onto their legs during territorial hovering displays and apply it to vegetation; this secretion is believed to attract females and repel other males. Like several other species of *Anthophora*, as well as some species of *Centris*, *Euglossa*, *Xylocopa*, and *Megachile*, males of *A. pilipes* have conspicuous tufts

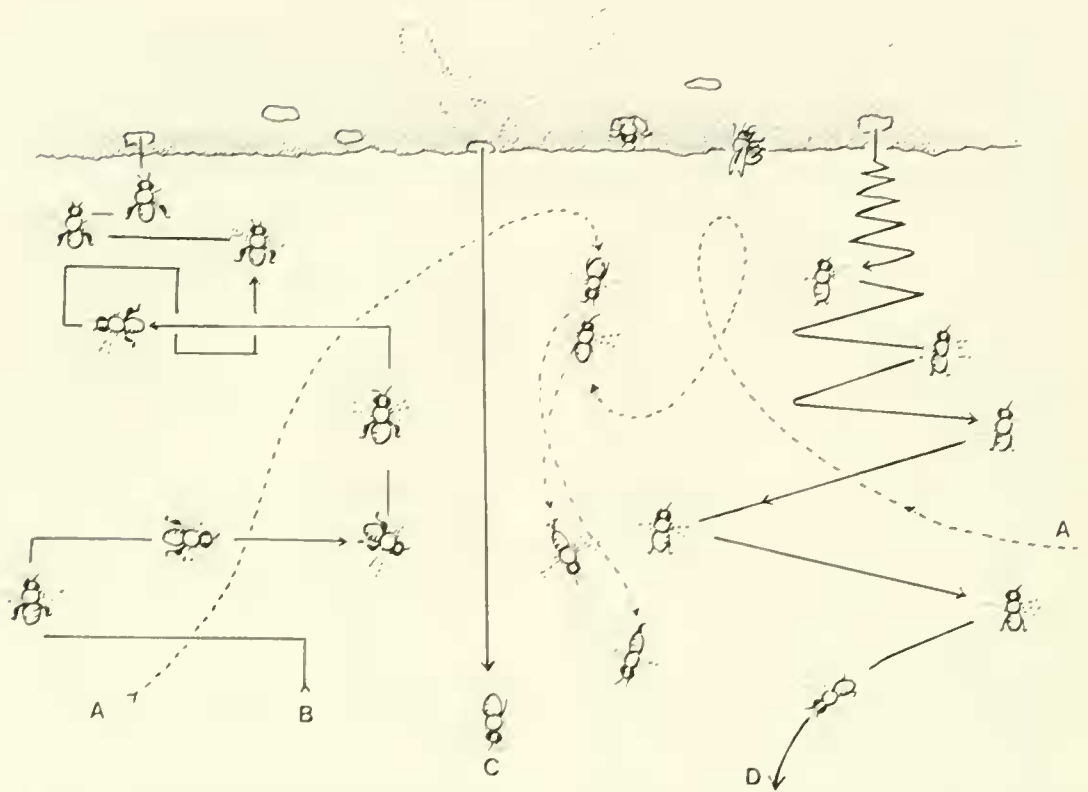


Fig. 3. Flight patterns in front of nests in an adobe block, as viewed from above. A, Flight paths of two territorial males (dotted lines) circling and confronting each other. The invader hovers to inspect a nest-excavating female, while rubbing his hind legs together. He is detected by the dominant male, is confronted, and is chased away within 30 seconds. As many as 10 males may simultaneously engage in such mutual pursuits and face-offs at the nest site. B, A returning forager approaches her nest while alternatively flying forward and hovering (sometimes turning to inspect nearby objects), forming a stepwise pattern. C, A forager precipitously leaves a nest that is occupied by two bees (the branches that were individually constructed by each bee are outlined). D, A female that has just selected the spot where she will start a new nest performs a rapid, jiggly orientation flight while looking at the spot and flying backwards in an expanding spiral until leaving the area.

Numerous males and females simultaneously perform these aerial maneuvers at the nesting site, with surprisingly few collisions (diagrammatic, from notebook sketches, not to scale).

of modified hair on their legs. The courtship behavior of *A. pilipes* suggests that these hair tufts serve as pheromone-carrying osmetrichia (Muller-Schwarze et al. 1977). The clypeal mustache of male *A. abrupta* carries pungent odors collected from plant sap (and perhaps also mandibular gland secretions), which are applied to objects to demarcate territories that are patrolled by several males (Norden and Batra 1985).

Male *A. pilipes* frequently rubbed their inner hind tibiae together in flight, while

hovering during their routine patrols, while pursuing a female, and when confronting another male (Figs. 4, 5). This motion, which is reminiscent of the scent-packing behavior of male *Euglossa*, was performed so often and so vigorously that the tips of the short, dense, stiff hairs inside the hind tibiae of old males became worn, with flattened tips, and the tight spiral structure of the hairs became unwound and the hairs straightened, as determined by SEM examination.

Patrolling males shared territories in



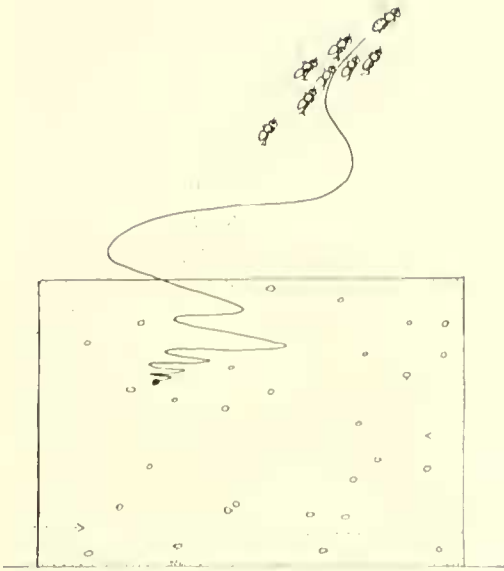


Fig. 4. Spiraling orientation flight (solid line) of a virgin female, leaving her natal nest for the first time. She at first faces the nest, then turns to leave, closely followed by a swarm of competing, buzzing, leg-rubbing males, which have abruptly abandoned their patrol routes (dotted lines) in front of the nests (diagrammatic, from notebook sketches, not to scale).

which they frequently chased each other in rapid, circling and zigzag flights. Often the pursued males briefly turned in flight to face their pursuers (Fig. 3). Several males were distinctively marked with dots of enamel paint. Thus, it was possible to determine that some males may become dominant over others for a short time, chasing them out of their territories whenever they flew into them. The dominant males may be replaced by other dominant males. For example, on April 15, 1990, four males were marked yellow (Y), green (G), white (W), and blue (B). On that day, B, Y, W, and several unmarked males sporadically patrolled the nesting area, where they occasionally pursued females as they left or entered nests. Male Y was most often present, followed by B and W; Y and B were seen fighting, as described below. By April 17, Y and G were present; on April 18, B and W were intermittently present; by April 21, Y, G, and W were all making



Fig. 5. Courtship. After pursuit and capture, the female's eyes are periodically rubbed by the flat brush of short hair, edged with long hair, on the extended, elongated mid tarsi of the male (arrows show motion). Above them, a second male similarly courts, while stretching his abdomen. The female is tightly clasped and her wings are held down by the male's sturdy, curved hind legs, which wrap tightly around her abdomen. The male's front tarsi rest lightly on her thorax. Three additional males approach, one landing and two vigorously rub their hind tibiae together, apparently to raise the short, stiff black hairs inside them for better purchase on the female. The mid tarsal brushes are simultaneously rubbed inside the hind legs during the approach. The front legs are folded during flight. (from photographs).

brief visits to the nest area, where females were starting to make their second nests. Male Y vigorously began to chase all the other males and aggressively pursued the females; and only Y had selected a revisited perch near the nest site. During this day, Y became increasingly aggressive toward other males and females, and he even chased other insect species away from this territory; he slept overnight in one of the nest holes. During April 22, Y (which was smaller than many other males) aggressively chased away G and other males, and several times he seemed to be scent-marking his perch at intervals of about 10 minutes, by touching it for less than one s each time. Many males had shifted their patrolling territories to the flowers where females were foraging, but Y continued to pursue and pounce on females

returning to nests. After April 26, Y had disappeared, to be replaced at the nest site by an aggressive, unmarked male, which chased away *Vespula* wasps, G and W. On April 27, W and G were seen fighting, and by that afternoon, W was dominant. Male Y once flew briefly into his former territory, but he did not stay. Male W was still present on April 28, and by May 1, all male activity at the nests had ceased. In 1989, a similarly dominant male (marked blue) was seen from April 19–27 pursuing, and fighting with, two other marked males, as well as with unmarked males. This individual dominated a territory near the nests from May 2–17, from which he chased all other males and a calliphorid fly.

Territorial display among the agile male *A. pilipes* consisted of rapid circling, twisting, and dodging aerial pursuits. These sometimes involved as many as 10 males simultaneously, thus being very difficult to observe. Usually, when a group of such males was in a territory near the nests, the entire loudly humming, shifting swarm rapidly spiraled up and out of sight; after a minute or so, these males returned singly, to resume their patrols and mutual pursuits near the nests. Males patrolling flowers also chased each other. The rapid activity pattern of a single, dominant, marked male (blue) on a warm day is illustrated (April 28, 1989: 12:20 EDT): hover in front of nests in territory, while rubbing hind legs together (H) 32 s; rest on perch in sun (R): 14 s; H 12 s; fly up, out of sight and return (F) 5 s; H 10 s; F 1 s; H 50 s; F 8 s; R 13 s; F 8 s; H 20 s; F 8 s; H 12 s; R 10 s; H 4 s; F 10 s; chased another male away (C) 10 s; H 30 s; F 20 s; H 39 s; R 23 s; H 26 s; R 73 s; C 2 s; H 35 s; R 48 s; H 39 s; R 17 s; C 50 s; (bee then left area temporarily).

Males not only chased conspecifics but also pursued other insects, causing them to leave the territories; these included bombyliid and calliphorid flies, *Polistes* and *Vespula* wasps, and nest-seeking *Osmia cornifrons* bees. Larger insects, such as bumble

bees and carpenter bees, were not pursued, although males were seen pouncing on a *Bombus* queen as she foraged in a patrolled area; she left the area after 10 hits. Territorial behavior may help prevent other insects from interfering with nesting female *A. pilipes* (female *A. pilipes* ignored other insects near their nests). Although males were contentious during the day, they slept together at night in empty nests and holes, including a keyhole. Males did not enter burrows to seek females. Sleeping in burrows was also noted by Miyamoto (1958) and Verhoeff (1892) observed males shoving for space in a sleeping hole.

Fighting among males seemed to occur infrequently. It began when a pursued male abruptly turned to face his pursuer, thus presenting him with the patch of pale facial hair and pale facial markings that distinguish males from females. Such hovering "standoffs" lasted only a few seconds, before one male either turned and flew off, with the other in hot pursuit, or, more rarely, the two insects collided audibly, grappled in midair and fell to the ground with a loud, harsh buzz. Then they immediately separated and flew up, one being chased rapidly away by the other. Individual territorial males hummed loudly, with the pitch of larger males being lower than that of smaller males; their pitch changed according to their flight patterns. It is unlikely that airborne sounds are perceived by bees (Fisher and Weary 1988).

Due to the males' nearly continuous diurnal activity, involving high-speed pursuits though gaps in vegetation, accidental collisions, fighting, and mating, the wings of males became frayed more rapidly than those of females. They eroded nearly as far as the marginal vein. As they aged, some broke their wing veins, thus dying because they could not fly to flowers to feed. Others, with eroded wing apices, flew more slowly and less often, with a lower-pitched hum. Aged males perched to sun themselves for longer periods than did young males and

they no longer aggressively patrolled or defended territories. Adult males did not live as long as females (40–48 days vs. 52–75 days maximum activity period for each sex). Although the females were engaged in arduous nest excavating and cell making tasks, the secretion of the energy-rich lipid cell linings and larval food, oviposition, and foraging for food and liquids, their wings wore less rapidly than those of males. Wing wear and mortality are positively correlated in bumble bees (Cartar 1992).

*Attraction to females:* Males throughout their lives vigorously and persistently displayed to, and courted, females of all ages, until their wings became too worn to permit them to rapidly follow the females. Male behavior suggested that copulation may normally occur in the tree canopy or at another high landmark away from the patrolled territory, after the close pursuit of a receptive female by one or more males. Copulation at the nest site or on flowers was not seen. Males were not attracted to empty cells from which females had emerged, nor to dead females, nor to females that were held captive in a net. However, when a female in a net was gently squeezed so that she emitted detectable mandibular gland scent, patrolling males flew upwind toward the net and hovered for 1–3 s where the scent was deposited. Males were also attracted for a minute to a box that had held virgin females, when it was first opened. Thus there seem to be both visual and chemical attractants. Although they seemed to be most strongly attracted to flying females (and flying males), they sometimes pounced on females that were resting, foraging or excavating nests. A courtship pattern that includes patrolling and close following flight was noted by Miyamoto (1958) and in a related species by Stone et al. (1988).

Males that were confined in the cages where they could be observed followed 10–20 cm behind flying females, while rubbing their hind legs together. When the females alighted, the males pounced on them, after

3–5 seconds spent hovering 5–15 cm behind these females. While hovering, the males hummed loudly, directed their antenna tips toward the females, and rubbed their mid-tarsal brushes against their hind legs. Simultaneously they rubbed their hind tibial brushes together, and also gently rocked their hovering bodies from side-to-side. After the males grasped the females, the pairs buzzed sharply, fell to the ground, and separated instantly, without any evident copulation.

Females with established nests were able to discourage unwanted male advances by raising their mid legs, by evasive flight, or more rarely, by confrontation. They did not leave nests when nuisance males were near them, or if they left, they flew out very quickly and directly. Females returning to their nests sometimes entered the wrong holes, as if to avoid pursuing males, or they dodged the males, making a distinctive sibilance during flight. Rarely, a pursued female abruptly turned around, hovered, and briefly faced the male, which caused him to instantly back away and fly elsewhere.

Male patrolling activity in the territory near the nests seemed to be determined in part by insolation, for there was more patrolling about mid-day when the sun shone on the site. Males patrolled flowers at other times of day. It was also influenced by the behavior of the females. Newly emerging virgin females, as well as females that were starting to excavate new nests (even if these were their second to fourth nests) exhibited slowly spiraling orientation flights that notably contrasted with the rapid, direct, purposeful nest departures and returns of females that had well-established nests. Males seemed to be attracted by this hesitant flight pattern, for they were most actively patrolling at the nest sites when virgin females were emerging, and again during the period when many females were starting their second nests.

Virgin females were closely observed as they first emerged from their natal nests, on April 7 and 8, 1991. Before females began



to emerge, males had been sporadically visiting the area during the previous 12 days. They flew past, briefly inspected holes, or two males chased each other in short bouts of 10–50 s, but all males were sometimes absent from the area for as long as a minute. When the females began to emerge, at least one male, and as many as ten or more males, remained constantly on patrol. Emerging dust-covered virgin females crawled out and rested near their nest entrances before their first flights. These stationary females, and virgin females still inside nests, were usually ignored by males. One such crawling female attracted a male, which hovered 1–2 cm behind her, vigorously rubbing his hind legs together, but she did not fly, and he flew away without contacting her. Most females, as soon as they began their initial orientation flights, were closely pursued by 1–10 loudly buzzing, frantically leg-rubbing, dodging males (usually all of the patrolling males), who followed their every movement (Fig. 4). A sibilant, hissing sound was emitted. Orientation flights began with the females hovering, facing their nests, then slowly spiraling in widening arcs upward and toward the sun (usually southwesterly). Departing females were detected within 3–10 s by the patrolling males. Although males followed all nesting females, the relatively slow departure of virgins permitted the males to maintain their close relationship in flight. When a chilled, immobilized, newly emerged virgin was placed at the nest site, she elicited a mating attempt that lasted 27 seconds. The male approached from behind, with vigorous rubbing of his hind legs, grasped her, and rapidly brushed her face with his hairy mid tarsi, but the female resisted him by raising her mid legs, pushing him away, and he departed.

*Courtship and copulation:* Mating was not observed until 1992, when I used five virgin females that were collected on emergence, chilled, and tethered by a thread tied between thorax and abdomen or held in forceps. Each female was swung back and forth

repeatedly at various speeds where a group of males was patrolling in front of an adobe nest block. The more rapidly the females were swung, the more numerous the males that were attracted, the denser became the swarm of males (resembling drones following a queen honey bee on a mating flight), the more closely they followed her, and the more vigorous were their attempts to grasp the female in "flight." Males ignored immobile females which were struggling to escape the forceps or thread, but were not swinging. Once males were attracted to a swinging female, they still attempted to mate when she was lowered to the ground. The attractiveness of females diminished after they had been exposed to the males for ca. two min. Males still followed swinging females and pounced on them, but they no longer grasped them firmly in attempts to mate.

During the few seconds' courtship (Fig. 5), a male firmly grasped the female's abdomen and held down her wings with his stout hind legs, which curled beneath her. (Probably the vigorous hind leg rubbing of males on approach to females serves to erect the stiff hairs inside their hind tibiae, to provide traction for grasping). He lightly rested his front legs on her abdomen or thorax. His slender mid legs were raised and fully extended above the female's head. The mid legs were jerkily waved up and down at a rate of ca. three times/s, so that the flat brush of hair on the mid tarsi stroked the female's compound eyes and antennae while he inserted his genitalia. During copulation, the male ceased rubbing the female's eyes, became quiescent, and leaned back with his mid legs raised, or stroking the female's thorax (1/s) for ca. 30–70 s, before abruptly flying away. Females were repeatedly mated and were sometimes courted by two or three piled-up males simultaneously. In Europe, Thalmann (1991) also observed that dominant males of *A. pilipes* in a greenhouse mated after a period of hovering near the female; they rubbed the females' eyes and

antennae with their mid tarsal brushes, and mating was repeated.

It is interesting that in *A. pilipes* the mid tarsi bear brushes that are used during courtship in the same manner as are brushes or ornately fringed, flattened areas on the specialized fore tarsi of certain megachilid bees (Batra 1978), carpenter bees, and sphecoid wasps (Low and Wcislo 1992). In these insects, these structures are used to cover the females' eyes or to gently rub them, producing a flicker effect and quieting them.

Some species in a genus (e.g. *Anthophora*) may have these structures, yet others lack them. Males of 52 of 81 species of Anthophorini surveyed bore brushes on their mid and hind tibiae or tarsi, but their function was unknown (Norden and Batra 1985). These are probably used for tactile and visual stimulation during courtship; they may also distribute sex pheromones during courtship and to delimit territories.

#### NESTING BEHAVIOR OF FEMALES

*Nest initiation:* Many females began to excavate their new nests during the same day that they had emerged from their natal nests and probably mated. The number of nests that were established during their period of emergence and the speed of female emergence were determined by the daily weather. For example, in 1991, 52 nests were started when a mass emergence of females occurred on April 8, which was an unusually hot, sunny day. In 1990, the weather was milder, the females emerged more slowly, and they established 42 nests during 11 days, which included four cool or rainy days (Fig. 2).

There was a strong preference among the bees to reuse nests that had been occupied in previous years, rather than to excavate fresh holes or to use artificially made holes, as in *Amegilla pulchra* (Smith) (Cardale 1968). Many holes were reused for four years. (In 1993, many bees preferred to creep under a white plastic sheet and wooden boards placed over five year old, eroding

nests, rather than move to adjacent new, exposed adobe blocks). In 1989, when there were no previous nests, the bees preferred artificially made holes as sites of nest initiation to the flat surfaces of the adobe blocks. During the following years, the bees first renovated existing nests in old adobe blocks and made branch tunnels from them (sharing an entrance); they also utilized artificial holes nearest to these natural nests; then they excavated nests beginning from the surface nearest to natural nests in old blocks; later, they dispersed to utilize artificial holes in new blocks away from natural nests; and least preferred was to excavate nests starting from the surface of the adobe of new blocks relatively far from the densest aggregation of occupied nests. This dispersal did not occur until the oldest adobe blocks seemed to have been filled to capacity with nests and the heavy traffic of flying bees was causing interference among them. Dispersal occurred in May, after the bees had already completed their first nests in the old adobe blocks.

The time needed by a female for the nest site selection process varied from a few minutes to several hours. Searching females hovered while facing the adobe surface, and produced a higher-pitched, "buzzier" hum than the smoother tones of foragers. They alighted frequently to enter existing nests, and to carefully inspect any cracks or holes in the surface of the adobe. For example, five marked females alighted 5–11 times per minute during their searches. During one three-min search, another marked female entered 11 established, occupied nests, leaving them promptly; she alighted on the pile of loose, excavated dirt at the base of the adobe four times, where she antennated and chewed it; she entered two artificial holes briefly, and once she chewed at a small depression in the adobe. Thus, a searching female may make hundreds of site inspections, and dig several shallow test holes, before selecting a nest location. Site selection seemed to be based on memory (of the

general location of her natal nest or of a previous nest); sight (attraction to any holes, cracks and depressions); and odor (attraction to the pile of dirt that was excavated by other females and to a container of such dirt removed five m from the nest area). Energy expended for careful nest site selection may later permit energy saving during the laborious nest excavation process. For example, one kg (dry weight) of loose earth, moistened, bitten, and scraped out by the bees, had collected below 70 nests at one site (14 g removed per nest).

Newly emerging, virgin females performed elaborate orientation flights, but females that were foraging, and females that had completed and sealed their nests, did not do so when departing. Instead, these latter females that had been busy sealing the last cells in their nests abruptly ceased doing so, hovered for a few seconds in the vicinity, and began immediately searching for nearby sites where their new second, third, or fourth nests would be excavated. During their searches, these bees often entered nests while occupants were present. Usually, the searcher departed immediately without any evidence of conflict. There was usually no tendency of searching females to take over partly provisioned nests during the owners' absences. Sometimes returning foragers briefly followed the hovering searchers, which caused searchers to leave the vicinity of the foragers' nests. Conflict was seen rarely, and it occurred when a nest seeker entered an occupied nest, or when she did not leave promptly enough on a forager's return. In these instances, loud, long, high-pitched buzzes were heard. The intruder was bitten and dragged, or shoved, out of the nest by the occupant. One intruder resisted ejection for two minutes by bracing her legs against the burrow walls. In another instance, a marked nest seeker (WO) was unusually persistent, and she succeeded in usurping a nest that was being excavated by an unmarked female (U), as follows (April 27, 1990): 10:32, WO searched for a nest site

as U dug a shallow hole; 10:37, WO pulled U out of the hole, both bees left the area; 10:38, WO returned, excavated the hole; 10:44, U returned, pushed WO out, dug; WO returned, pushed U out, dug, U hovered; U pushed WO, WO raised hind legs, kept digging; U left area; returned, bit WO abdominal area; WO left, hovered, U dug; 10:47, WO grabbed U, knocked her out of hole; WO dug, U hovered, then pulled out WO by abdominal hairs, U entered hole; WO returned, grabbed U; both bees fell out; WO returned to hole; 10:48 U pulled out WO by hairs, both fell, U in hole; WO returned, pulled out U, both fell; WO in hole, pulled out by U (twice); U in hole, dug, was pulled out by WO, both bees fell, buzzed, clasped, bit each others' legs; WO in hole, U pulled her out, both fell (repeated twice); U in hole, WO pulled her out (twice); U hovered, then began to seek another nest site; 10:50, WO making the hole deeper; 10:50-10:52, searching U touched WO twice but did not pull her; 10:55, WO left the hole with a prolonged orientation flight, indicating that she had selected it as her nest. By 11:02, U had started a new nest elsewhere. This example is presented at length due to its rarity. This is contrary to the frequent usurpation and fighting among European *A. pilipes* noted by Van Lith (1947). The usual passivity of the Japanese subspecies often permits two females to share a single entrance without conflict. Many holes led to two branch tunnels, with each tunnel leading to a series of cells constructed independently by each female (Fig. 3). These shared nest entrances became more common as the season progressed. The apparent leveling-off in the number of new nests constructed, based on counts of nest entrances, was partly due to the increased sharing of nest entrances (see below). There were more nests than entrances, especially late in the season (Fig. 2).

When a searching female had evidently decided on a nest site, after having chewed at the soil for 2-6 min, perhaps marking it



with her mandibular gland secretion, she performed a prolonged orientation flight, at first hovering briefly before her selected spot, then spiraling up and away (Fig. 3), to return after 2–7 min with a load of liquid to moisten and soften the adobe for further excavation. Subsequent departures involved no orientation flights, the site having already been memorized. The site of any previous nest was forgotten after it was sealed, when searching behavior was initiated. This ability to learn new locations for nests would be beneficial for growers, who may be required to move pollinator colonies occasionally. Usually, once a site was selected, the bee continued to excavate. In a few instances, females abandoned partly-excavated sites for others, after making several liquid-collecting trips and after digging several mm (one abandoned hole was made into a nest the following year). Evidence that site memorization occurs during the spiraling orientation flight was provided when a marked orientating bee that was just leaving a newly selected site bumped into a returning forager. The memorizing bee immediately ceased her orientation flight, and resumed her search for a new nest site, without any noticeable attraction to the site that she had just selected and had begun to memorize; evidently she became confused by the collision.

*Excavation and construction:* Nest excavation required frequent trips to collect liquid, which was regurgitated to moisten and soften the dry, hard, red clay adobe. Houston (1991) suggested that the anthophorid *Amegilla dawsoni* (Rayment) may use nectar to moisten and soften soil for nest excavation because free water was not available in their desert habitat. Although plenty of water as dew, raindrops, puddles and in shallow trays was available to *A. pilipes* in cages and near nests in the field, females were not seen collecting it. This was surprising, because *A. abrupta* and other species drink water for nest construction. I placed bits of soil that had been orally

moistened by excavating females, and to me tasted sweet, on water-moistened Dextrostix glucose oxidase-chromogen blood glucose test strips, to test for sugars. These always gave a strong positive reaction, suggesting that these bees may be using nectar to moisten soil. The same test strips did not react with soils that had been moistened by *A. abrupta*, a species that is known to collect water. Pollination would be accomplished by *A. pilipes* when gathering nectar for use in nest construction, an additional benefit of this species. Twenty-six liquid-collecting trips lasted 2–11 minutes, and deposition of the liquid during the nest excavation between trips lasted 3–5 minutes. Excavation was accomplished by the mandibles, and the loosened soil was raked out primarily with the forelegs. The scopae of excavating females often became filled with mud and dust. Females that were returning with a load of liquid sometimes flew up to their nests with their glossae extended, as if they were approaching flowers. The rate of nest excavation varied, perhaps because the adobe was not of uniform texture. The bees generally excavated at the rate of one mm in depth per 2–4 minutes, including the flight time needed to collect liquid. Excavation consisted of alternately extending the glossa, to release a droplet that moistened the soil, then taking 5–10 rapid bites, with the tongue folded and head nodding. During excavation, the females produced series of sharp, distinctive quack-like chirps, audible from 1–2 m. Probably these vibrations helped to loosen the soil. This cycle was repeated until more liquid was needed. Fifteen of 20 nests that were excavated from the surface (not renovation of old nests), were completed and ready for provisioning during fair weather within 24 hours of the initial selection of their sites, but five nests required one or two days for excavation. The most rapid progress was a nest that was completely excavated, with provisioning begun, within seven h at 25–29°C.

The shallow nests, which consist of a se-

ries of about four ovoid cells, were described by Torikata (1931) and Van Lith (1947). Cells are lined with an opaque, whitish waxy layer and emit a nauseating odor (Van Lith 1947). In *A. abrupta*, the cell lining is made of diglycerides and odoriferous butyric acid, secreted as triglycerides from the abdominal Dufour's gland; these secretions are also added to the semiliquid provision (Norden et al. 1980). The multilobed Dufour's gland of actively nesting *A. pilipes*, like that of *A. abrupta*, occupies about 70% of the abdominal cavity. Nests and provisions of *A. pilipes* in the adobe blocks emitted a pungent, unpleasant butyric odor discernible from four m away; it was similar to that of *A. abrupta* and fermenting oak sap or vomit. During warm evenings, this odor attracted ambrosia beetles (Scolytidae).

*Provisioning, oviposition, and closure:* Pollen-collecting trips lasted 6–47 min. They were in series, or alternated with one or several return trips without pollen. Observations of pollen load color and pollen analyses showed that many females collected pollen from more than one host during a single foraging trip, or switched hosts during a day or more. Departing foragers precipitously lurched from their nest entrances, often falling 2–4 cm to gain momentum before taking flight. Those that left nests near the bases of the adobe blocks sometimes tumbled onto the ground. There were no orientation flights by foragers, which departed directly and swiftly. Returning foragers usually entered nests directly or after periods of hovering in a stepwise pattern (Fig. 3). They appeared to be unusually inquisitive for insects, and often hovered to inspect the observer and other bees, turning to face them. At very low light levels (600 lux), hovering became prolonged, flight became slow, humming took on a low pitch, and returning foragers often alighted near their nests, to which they crawled.

Total time spent in cells to deposit nectar and pollen loads ranged from 2–9 min. It was possible to observe provisioning in those

cells that were located near the surface. Foragers entered head first, deposited their nectar for 30–60 seconds while pumping their abdomens, quickly turned around, scraped the pollen from the scopae on their hind legs for 30 seconds, then slowly rotated for 2–2.5 min in the cells several times in both directions (about once per 10 s), while making rapid tamping motions with their abdomens. The pygidial plate was evidently being used to compress and mix the provisions. Dufour's gland secretion probably was also added at this time (probes that were dipped into cells that were being provisioned removed samples of wet pollen that had a strong, butyric odor). Bees sometimes then quietly rested, looking out of their cells, for 40 s to five min, before rotating their heads, protruding their tongues, and abruptly leaving for another foraging trip. Oviposition was cryptic, brief, and could not be observed without disturbing the bees. It occurred during a rest period as described above, and was indicated because the female next began sealing the cell instead of leaving for another foraging trip.

The process of cell sealing includes behavior patterns similar to those used by other *Anthophora* species during cell construction. After the pause for oviposition, females immediately began to chew at the nest entrances while licking these areas to wet them. Chewing and licking (with folded glossas) alternated, while the bees' heads bobbed about 10 times per second. Meanwhile, the bees also rotated in both directions (10–20 s rotation) as they rapidly tamped down the soil that had been wetted and loosened by their mouth parts and shoved back by their legs. Bees rapidly vibrated their pygidial plates (ca. 10 tamps s) to compress the soil, gradually forming the smooth, shiny, wet exterior of the cell caps. As cells neared completion after some 20 minutes, tamping continued, but biting and licking ceased. Bees occasionally paused, with waving antennae, to rest, or groomed themselves. The cell cap formed the bottom of the next cell

in the series or served to seal the nest, if the cell was near the surface and there was no more space for another cell. In that case, bees abruptly ceased tamping, and flew off to seek a new nest site.

*Nest occupancy:* The patterns of construction and renovation in 63 numbered nest entrances were observed from April 18 through May 31, 1990. The movements of 18 females that had been individually marked with dots of paint were tracked as they constructed, provisioned and sealed nests, then moved on, to begin new nests.

Thirty-three of the 63 nests had been started before April 18. These primary (the first nest made by a bee) nests were inhabited by their original residents for as long as 31 days. Thirteen of them were reoccupied by another bee within 24 h to 19 days after they had been abandoned by the original residents. (Many original bees went elsewhere to begin another nest). These bees stayed for 3–19 days, making secondary nests. Some could be seen excavating a branch tunnel just inside the nest entrance (Fig. 3). Three of these 33 nests were subsequently reoccupied by a third bee, after having been vacated by the second bee for 1–8 days. These tertiary nest occupants stayed for 6–21 days.

The complete cycle of nest initiation, construction, provisioning, completion, and abandonment (perhaps with reoccupation) was observed in the remaining 30 nests that were started on or after April 18. Their original constructors and inhabitants stayed for 3–26 days. Twelve of these 30 nests were reoccupied by a second bee after lying vacant for from under 24 h to 19 days. Two of the 30 nests were later to be occupied by a third bee.

As nest entrances were occupied and reoccupied by many bees during up to five years, they became wide and irregular. For example, nests that were first excavated in 1989 were preferred sites for re-nesting during the next four years. Some may thus have been home to as many as 12 active, repro-

ducing females: one in 1989, two in 1990, three in 1991, 1992 and 1993. Nest entrances were never repaired or otherwise attended to by *A. pilipes*.

The 18 individually marked females made a total of 30 nests; 11 of them made only one nest. However, three made one extra nest, three made two extra nests, and one made three extra nests. These latter bees thus made 12 supplemental nests, in addition to their original nests. Seven of these supplemental nests were also secondary nests, having been made in existing nest entrances made by another bee; the remaining five nests were begun 'from scratch'.

Because the adobe was not broken up in order to count total cells, the contribution of each type of nest to reproduction was not determined. It was more important not to disturb as many bees as possible, in order to maximize their survival. The sharing of nest entrances and the construction of multiple nests by individual bees made it difficult to estimate the total population by counting nest entrances.

#### CONCLUSION

*Anthophora pilipes villosula*, the "shaggy fuzzyfoot bee" is highly recommended for management and development as a pollinator of spring-blooming crops in warm, humid temperate climates. This gentle, gregarious bee is tolerant of human activities, perhaps having been associated with people in caves and houses for millennia. It forages for food, nest provisions, and nectar used in nest building, from before dawn until after dusk, and in inclement weather. It nests in inexpensive adobe blocks that may be easily handled and stored during the bees' long dormancy.

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